Chapter 9

Spatial and Temporal Analysis of Transoceanic Shipping Vectors to the Great Lakes

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Anthropogenic introductions of nonindigenous species (NIS) are predicted to impact biodiversity of lakes more than any other major ecosystem type over the coming century (Sala et al. 2000). Freshwater ecosystems are highly vulnerable to invasions by NIS because of their close association with human activity, including exploitative uses for municipal and industrial water supplies, natural resource development (e.g., fishing, aquaculture), and commercial navigation and recreation. These varied uses provide countless invasion opportunities for NIS throughout the world. Consequences of these invasions have become well characterized, as many of the world's large lakes have been colonized by infamous nuisance invaders such as Nile perch (*Lates niloticus*), zebra mussels (*Dreissena polymorpha*), water hyacinth (*Eichhornia crassipes*), and hydrilla macrophytes (*Hydrilla verticillata*). Profound changes to the physical, chemical, and biological properties of lakes have followed invasions by these and other species of invertebrate and vertebrate animals, and micro- and macroscopic plants (e.g., Zaret and Paine 1973, Oliver 1993, Spencer et al. 1999, Ketelaars et al. 1999, MacIsaac 1999, Vander Zanden et al. 1999, Hall and Mills 2000, Lodge et al. 2000, Donald et al. 2001, Dick and Platvoet 2000, Schindler et al. 2001, Vanderploeg et al. 2002).

NIS are introduced to lakes through both intentional and inadvertent vectors. Government-sponsored stocking programs are the leading intentional vectors. Historically, many species of fishes were added to lakes around the world in an attempt to create fisheries where they previously did not exist (e.g., in fishless alpine lakes), to enhance preexisting fish stocks (e.g., through introductions of *Micopterus* spp. and *Lates nilotica*), or as a biological control agent of insects, snails, or nuisance plants (e.g., introductions of *Gambusia*, *Mylopharyngodon*, or *Cyprinus*) (see further discussion by Fuller in this volume, and references therein). Stocking of predatory Nile perch (*Lates niloticus*) into Lake Victoria represents one of the greatest evolutionary and ecological disasters precipitated by mankind, as up to 200 species of vulnerable endemic cichlid fishes were subsequently driven to extinction (Kaufman 1992).

Invertebrates have also been widely stocked to lakes throughout the world, typically with the intention of enhancing food supplies available to fishes. Crustaceans, such as amphipods, mysids, and crayfish, have been stocked most commonly, sometimes with catastrophic consequences. For example, mysids were stocked into lakes in Scandinavia, Kootenay Lake in British Columbia, and Flathead Lake in Montana. Amphipods and mysids were also introduced to many lakes in the former Soviet Union between 1940 and 1960, although the practice appears to have waned in recent years (see Grigorovich et al. 2002). The Baikal amphipod *Gmelinoides fasciatus* was first stocked in the Volga River system during the early 1960s, and later to many other lakes throughout western and northern Russia. It established in western Russia in Lake Ladoga in the early 1980s, and is now abundant in that system (Panov 1996). Rather than augmenting the food supply available to fishes in these systems, mysids can compete for zooplankton prey with young-of-year planktivorous fishes, often causing a collapse of the very fish populations they were intended to enhance (see Spencer et al. 1999). Stocking or aquaculture programs may indirectly facilitate introduction of other, nontarget species that parasitize, infect, or are similar in appearance to target species (Grigorovich et al. 2002).

Shipping activities constitute a very important vector for the inadvertent introduction of NIS to coastal marine habitats and some freshwater systems, such as the Laurentian Great Lakes of North America (e.g., Carlton and Geller 1993, Ruiz et al. 2000a, 2000b, Ricciardi 2001, Leppäkoski et al. 2002). Ships traveling between the world's ports have long employed ballast for stability and trim when traveling without cargo. Initially, solid materials were loaded as ballast (e.g., sand, soil, rock), which resulted in dispersal of seeds of many terrestrial and wetland plants (see Mills et al. 1993). Water replaced solid materials as the dominant ballast medium around 1900, resulting in the transport and release of many waterborne aquatic taxa (see Mills et al. 1993). Ballast water was the dominant vector of NIS to the Great Lakes between 1960 and 2001, a trend that has been accompanied by a dramatic increase in the number of new invaders (Mills et al. 1993, Ricciardi 2001, Grigorovich et al. 2003a).

Shipping interacts with the creation of dams and canals, which alter hydrology to provide access to new watersheds and thereby facilitate dispersal of NIS. For example, the Caspian Sea was invaded in 1999 (or earlier) by the ctenophore *Mnemiopsis leidyi*, which was likely introduced from the Black Sea or the Sea of Azov by a ship utilizing the Volga–Don Canal. This canal, which was opened in 1952, connects the Black and Azov Seas with the Caspian Sea (Ivanov et al. 2000). Similarly, invertebrate species have dispersed to the lower Rhine River and the Baltic Sea via a series of connecting rivers and canals within Europe (reviewed in bij de Vaate et al. 2002). In the Great Lakes basin, creation of canal systems along the St. Lawrence and Niagara Rivers has likewise facilitated dispersal of NIS from lower to upper lakes (Mills et al. 1993).

Certainly many other vectors contribute to the global transfer of species, the relative importance of which varies from system to system and over space and time. For example, release of sport baitfish and other organisms resident in bait water may result in establishment of NIS in systems utilized by anglers (Litvak and Mandrak 2000). Sport fisheries and pleasure boating may also result in inadvertent invasions if macrophytes and attached invertebrate fauna are stranded on boat trailers moved between systems (see Johnson et al. 2001). Releases of unwanted aquarium pets or live fishes intended for human consumption can also result in invasions (e.g., Fuller, this volume).

Efforts to prevent new invasions require an understanding of the invasion process, particularly the sources and mechanisms of propagule supply. In this chapter, we review the present state of knowledge of NIS transfer and invasion patterns in the Great Lakes, focusing especially on ship-mediated transfer.

Vectors to the Great Lakes

The Great Lakes are an excellent model system with which to analyze invasion vectors (MacIsaac et al. 2001). The system is well defined and studied, allowing for identification of invasion vectors and pathways, and is similar to many estuarine ecosystems and large inland water bodies where shipping dominates vector supplies of NIS. The lakes also serve as a gateway to invasion of adjacent inland lakes through a host of other vectors associated with human activities (e.g., see Johnson et al. 2001, Borbely 2001).

At least 162 NIS are established in the Great Lakes proper (Ricciardi 2001, Grigorovich et al. 2003a). All of these species are characteristic of lentic ecosystems, including a broad spectrum of organisms from phytoplankton to fish. The reported establishment rate of new NIS increased linearly between 1959 and 1989 at an annual rate of 0.621 new species; however, this rate accelerated to 1.880 new species per year (95% confidence interval: 1.543–2.216) between 1989 and 2001 (Grigorovich et al. 2003a). Many of the NIS that invaded the Great Lakes in recent years originated from Europe, notably the Baltic Sea and lower Rhine River areas (Ricciardi and MacIsaac 2000, bij de Vaate et al. 2002, Grigorovich et al. 2003a). For example, allozyme and mitochondrial DNA analyses have pinpointed the origins of Great Lakes populations of *Bythotrephes longimanus* and *Cercopagis pengoi* water fleas to the Baltic Sea region, and of *Echinogammarus ischnus* amphipods to the lower Rhine River (Berg et al. 2001, Cristescu et al. 2001, M. Cristescu, unpublished data). Internal waterways in Europe have facilitated the dispersal of species from the Black and Azov Seas to the Baltic Sea and lower Rhine (see bij de Vaate et al. 2002). Once established in major ports in western and northern Europe, Ponto-Caspian and other Eurasian species invade the Great Lakes in secondary invasions mediated by ships' ballast water (Ricciardi and MacIsaac 2000, bij de Vaate et al. 2002). A spate of ballast-mediated invasions by Ponto-Caspian species has transformed Great Lakes species communities in recent years (Ricciardi and MacIsaac 2000).

The Great Lakes currently receive NIS propagules from ballast tanks in two distinctive forms. First, they receive large volumes of water from each of a relatively small number of ships that enter the lakes loaded with saline ballast water (ballast-on-board or BOB ships). The introduction of biota in ships' ballast is not surprising, given the vast amount of water imported in this way. For example, in 1995 the Great Lakes received an estimated 5×10^6 m^3 of ballast water per year from oceangoing ships (Aquatic Sciences 1996). Canada implemented voluntary ballast water exchange regulations covering the Great Lakes in 1989. These regulations were made mandatory, effectively covering the entire Great Lakes basin, by legislation implemented by the U.S. Coast Guard in 1993 (U.S. Coast Guard 1993). Regulations require that vessels entering the lakes from foreign locations treat low-salinity ballast water before discharging into the Great Lakes. The only treatment identified to date consists of ballast water exchange, whereby ships flush their tanks while traversing open ocean to purge most organisms from their tanks, and to kill remaining freshwater organisms by osmotic stress (Locke et al. 1991, 1993, U.S. Coast Guard 1993). While this treatment reduces populations of freshwater organisms resident in ballast tanks, its efficacy is not complete (Locke et al. 1993, MacIsaac et al. 2002).

A large percentage of ships enter the lakes loaded with cargo (no-ballast-on-board or NOBOB ships) and carry only residual ballast water (i.e., 50–60 tons) and sediment. These vessels fill their ballast tanks with Great Lakes water when they discharge cargo in port. Great Lakes water loaded by these ships mixes with the "residuals." The mixed slurry is then discharged at a subsequent port, often on the Great Lakes. This ballasting activity is entirely legal, though it may predispose the Great Lakes to invasion by taxa living in ballast residuals or by their viable resting stages (Bailey et al. 2003; C. van Overdijk, unpublished data).

It is not clear why the reported invasion rate of the Great Lakes accelerated during the 1990s. Possibilities include greater attention and more researchers studying invasion phenomena, lag periods between introduction of NIS and their first reported discoveries in the system (Grigorovich et al. 2003a), or changes in vector supply (Carlton 1996).

Here we provide an overview of NOBOB ships as a potential vector to the Great Lakes. Our objectives are to (1) assess temporal variation in intensity of transoceanic ship traffic entering the lakes; (2) assess the relative frequency of transoceanic ships entering the entire system loaded with saline ballast water (BOB ships) or loaded with cargo and only residual water and sediments in ballast tanks (NOBOB ships); (3) determine the relative frequency of BOB and NOBOB vessels to each of the lakes, and compare these patterns with the establishment sites of recent invaders to the system; (4) characterize the regions of origin for NOBOB vessels and contrast this pattern with the recent invasion history of the Great Lakes. Overall, our intent is to gain a rough understanding of potential supply of NIS to the lakes by ships, using ballast activities as a proxy.

Great Lakes Shipping Profile

We compiled information on commercial ships originating from foreign ports and inbound to the Great Lakes from the period 1994–2000, using compiled reports on annual ship arrivals (Eakins 1995, 1996, 1997, 1998, 1999, 2000, 2001). We supplemented these data with shipping information collected by the St. Lawrence Seaway Management Corporation for 1986 through 1998 (C. Major, pers. comm.) to determine global ports of origin for ships visiting all ports on the Great Lakes. Both sources of data were used to build a comprehensive database of ship activity for all inbound ships during 1997, including port and country of origin, ports visited on

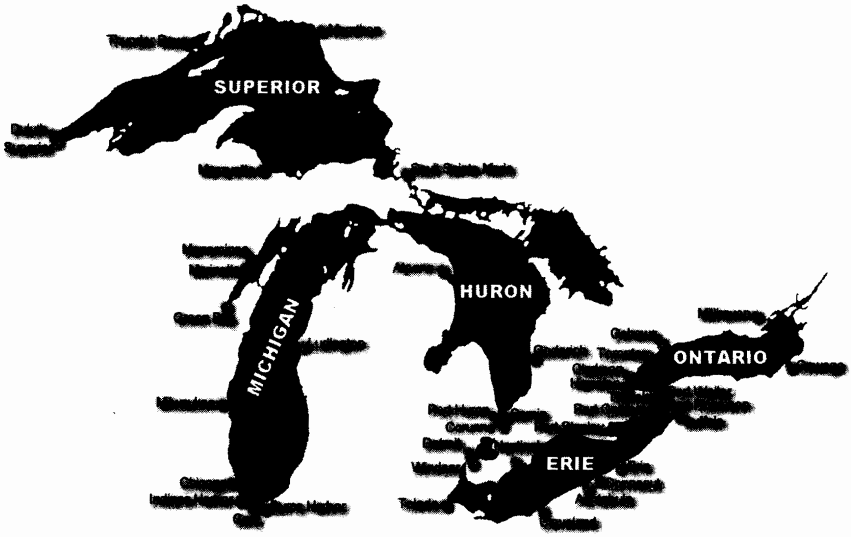

FIGURE 9.1. Location of major Great Lakes ports visited by foreign, transoceanic ships between 1986 and 2000. Ports on the St. Lawrence River were excluded from the study.

the Great Lakes (Fig. 9.1), and their ballasting/deballasting activities while operating on the Great Lakes; additionally, we determined whether ships entered under BOB or NOBOB status.

We selected 1997 to provide detailed analysis of vector traffic to the Great Lakes, although there appeared to be minimal variation in patterns between 1994 and 2000. We determined the last port of call (i.e., the last port that a vessel visited prior to entering the St. Lawrence Seaway) for all ships that entered the Great Lakes during 1997 (Table 9.1).

We classified vessels based on their ballast water status when entering the Great Lakes. In most cases, oceangoing ships that entered the lakes in NOBOB status deliver cargo and also load cargo before leaving the Great Lakes. Although such vessels load ballast water while in transit on the lakes, we continued to classify these vessels as NOBOB ships to distinguish them from those that entered the lakes with saline ballast water.

We made the following assumptions regarding ships' ballast water management activities:

- All vessels that deballast at their first port of call (BOB ships by definition) discharge only ballast water of oceanic origin, in compliance with existing regulations (U.S. Coast Guard 1993).
- All vessels that discharge cargo at their first port of call are in NOBOB

TABLE 9.1. Last country of origin and final port of call for NOBOB ships entering the Great Lakes during 1997.

NOBOB Vessels' Country of Origin	*Lake*				
	Superior	*Huron*	*Michigan*	*Erie*	*Ontario*
Belgium	33	1	4	2	1
Netherlands	8	2	6	4	4
Baltic Sea (German and Swedish Baltic ports)	58	2	5	4	3
Germany (North Sea ports)	8	0	0	1	0
Sweden/Norway (North Sea ports)	2	1	1	0	0
Mediterranean/Atlantic Europe	35	0	7	0	2
U.K.	8	1	5	0	0
Latin America	20	1	0	2	2
Brazil	12	0	0	3	0
Japan/China	5	0	0	1	1
Australia	16	0	0	2	0
South Africa	9	0	0	0	1
Ukraine	4	0	0	0	0
Romania	2	0	0	0	0
Indonesia	1	0	0	0	0
U.S.A.	0	2	0	0	0
Canada	0	0	0	1	1
Other European	0	1	0	0	0
Unidentified	7	1	0	1	0
Ballasted ships	15	3	0	6	1

Note: All vessels are assumed to have loaded and subsequently discharged Great Lakes water as ballast in one of the Great Lakes. Nine ships' records were discarded owing to lack of information pertaining to the Great Lake in which ballast water was discharged. Thirty-six ships visited two European ports, and three visited three European ports, prior to arriving in the Great Lakes; each port and country visited by these ships was tabulated separately because the order in which the ports were visited could not be ascertained. Ballasted ships carried (saline) water to the Great Lakes. Vessels arriving from German and Swedish ports were subdivided into those from the Baltic Sea and from the North Sea.

condition (i.e., they had no exchangeable ballast upon entering the Great Lakes).

- All vessels load some freshwater ballast at each Great Lake port where they discharge cargo, and discharge ballast water at subsequent ports on the Great Lakes (if any) where outbound cargo is loaded. Where ships loaded cargo at two consecutive ports, ballast values of one-half were given for each port. No ships were observed that loaded cargo at more than two ports in a single trip. NOBOB vessels are assumed to load Great Lakes water as ballast because cabotage legislation prevents foreign vessels from loading new cargo for transfer within the system to ports in the same country. We found no records of interlake movement of North American cargo by foreign NOBOB vessels.

- NOBOB vessels that leave the lakes without loading cargo for their outbound trip do not discharge ballast water loaded while operating on the Great Lakes.
- Ballast water discharges associated with particular ports are ascribed to the downstream lake basin. For example, discharges at Sault Sainte Marie were ascribed to Lake Huron, whereas those in the St. Clair and Detroit Rivers were considered to occur in Lake Erie. Ballast water discharged at Port Huron, Michigan, and Sarnia, Ontario, were deemed to occur in Lake Erie, and those in the Welland Canal (near Port Weller) were ascribed to Lake Ontario (Fig. 9.1).
- A uniform volume of ballast water is released by each ship operating within the Great Lakes, regardless of ship size, cargo, or other factors. This is similar to the approach of dividing ballast discharge evenly among ports loading cargo (above).

Our estimate of "propagule pressure" is admittedly coarse. It assumes that ballast water discharge patterns can be determined by the cargo loading patterns and that the density of organisms contained in ballast water of different ships is invariant. Ships arriving from different source regions may load different densities of live organisms in ballast water. Carlton (1985) and Ruiz et al. (2000a) reported that survival of organisms in ballast tanks is strongly time-dependent. Thus, variability in the number of viable propagules could be quite high depending on the duration of the trip, the source region, and the efficacy of ballast water exchange prior to entering the Great Lakes.

We have not included any information on ports on the St. Lawrence River that were visited by inbound ships, nor have we tracked the destination of Great Lakes ballast water loaded by NOBOB vessels that leave the lakes without discharging water. Many of these vessels visit ports on the St. Lawrence River on their outbound journey, and likely discharge water at these sites (R. Colautti, unpublished data).

SHIPPING AND BALLAST WATER DISCHARGE PATTERNS

The volume of inbound traffic to the Great Lakes by foreign vessels has varied tremendously over the past twenty-two years (Fig. 9.2). Traffic has

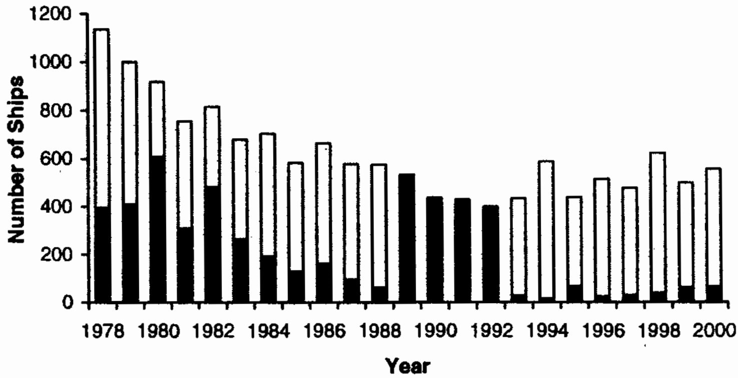

FIGURE 9.2. Total number of foreign, transoceanic vessels entering the Great Lakes through the St. Lawrence River system between 1978 and 2000. Ships carrying ballast water into the lakes (black bars) have declined both in absolute number and relative to those entering with cargo (NOBOB ships; white bars). Years for which no distinction was made between vessel types are shown in gray bars.

declined since the late 1970s, and has remained more or less stable during the past fifteen years, with some variability likely correlated to global economic activity. The fraction of inbound ships loaded with ballast water has strongly diminished in recent years, corresponding with enhanced economic efficiency of shipping companies during the late 1980s and the 1990s. Consequently, both the absolute number and the proportion of foreign ships entering the Great Lakes carrying ballast water (BOB ships) diminished sharply over the past twenty-five years, though both appear to have leveled off in recent years.

Inbound traffic to the Great Lakes between 1986 and 1998 was dominated by ships arriving from European ports, notably those in the lower Rhine River region (i.e., Belgium, the Netherlands), other localities on the North Sea (i.e., Germany, Norway, Denmark), and the Baltic Sea (i.e., Latvia, Lithuania, Poland, Estonia, Germany, Sweden, Russia, Finland) (Fig. 9.3). However, it is difficult to interpret these data since many of the vessels, particularly those from the late 1980s onward, arrived to the Great Lakes under NOBOB status. For these vessels, the last port of call was more likely to be a ballast water recipient than a ballast water donor. For example, Antwerp, Belgium, is one of the leading ports serving the Great Lakes, but most vessels originating at this site loaded cargo and potentially discharged ballast before departure. Collectively, the top ten vessel source regions represented an average of 88 percent of all inbound traffic to the Great Lakes.

We analyzed data on the movement of cargo to and from ships operat-

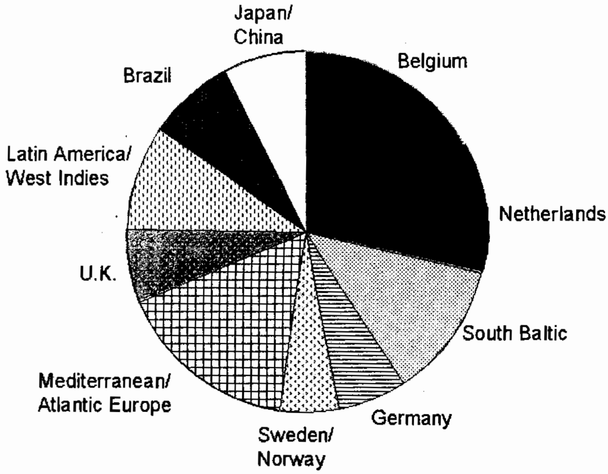

FIGURE 9.3. Average percent contribution of commercial ships entering the Great Lakes between 1986 and 1998, for the ten leading countries or regions, based upon last port of call.

ing at their first ports of call on the Great Lakes to infer their status as BOB or NOBOB. Between 1994 and 2000 inclusive, an average of 8.1 percent of foreign vessels bound to the Great Lakes declared BOB status (Table 9.2). A large fraction of these vessels (55.4%) proceeded directly through the lower lakes and discharged (saline) ballast water in Lake Superior. Lakes Ontario (17.4%) and Erie (17.9%) averaged fewer direct discharges of ballast water by inbound BOB ships than did Lake Superior, despite being the first lakes in the system (Table 9.2).

The first port of call for most NOBOB vessels entering the Great Lakes between 1994 and 2000 was located on Lake Ontario (40.6%) and Lake Erie (43.1%). Lake Superior was the initial port of call for only a very small fraction of inbound NOBOB vessels (0.6%). By contrast, the pattern of ballast water discharge by BOB and NOBOB vessels was focused on Lake Superior (Fig. 9.4). The majority of NOBOB vessels deballasted in Lake Superior (74.5% of total), irrespective of whether these ports represented the second, third, or final port of call. In 2000, for example, a total of 397 ships visited a second port on the Great Lakes after having off-loaded cargo at their first ports of call. Of these, approximately 37 percent proceeded to ports on Lake Superior where they loaded cargo (and presumably discharged ballast water) for their outbound voyage. An additional 13 percent loaded cargo at other Great Lakes ports, and 199 ships off-loaded cargo at their second port of call and continued on. Of the 199 ships that off-loaded cargo at their second port, 29 left the Great Lakes without loading cargo for their return trip, and 170 continued to a third port on the Great Lakes.

TABLE 9.2. Distribution of ships entering the Great Lakes that either discharge ballast water or discharge cargo at their first port of call.

	Ships per Year Entering the Great Lakes						
Ship Entry Type	*1994*	*1995*	*1996*	*1997*	*1998*	*1999*	*2000*
Ballast	15.0	67.0	24.0	28.5	39.0	62.0	64.0
Erie (%)	16.7	17.9	37.5	24.6	20.5	12.9	10.9
Huron (%)	0.0	4.5	0.0	0.0	5.1	0.0	10.2
Michigan (%)	16.7	7.5	0.0	0.0	5.1	4.8	6.3
Ontario (%)	20.0	22.4	29.2	19.3	23.1	8.1	11.7
Superior (%)	46.7	47.8	33.3	56.1	46.2	74.2	60.9
NOBOB	572.0	372.0	489.0	447.5	583.0	435.0	490.0
stayed (%)	67.3	69.9	68.9	74.0	74.7	77.7	81.0
departed (%)	32.7	30.1	31.1	26.0	25.3	22.3	19.0
TOTAL SHIPS	587.0	439.0	513.0	476.0	622.0	497.0	554.0

Note: All ballast water discharged at the first port of call is considered saline, in compliance with extant regulations (U.S. Coast Guard 1993). All ships that discharge cargo at the first port of call are considered NOBOB. NOBOB ships were classified into those that stayed within the Great Lakes (see Fig. 9.4) and those that departed the system, without deballasting at any port, following off-loading of cargo. Ships arriving with ballast water were categorized by the lake that ultimately received discharged water. Percentages are rounded off. (Source: Eakins 1995, 1996, 1997, 1998, 1999, 2000, 2001.)

Almost 50 percent of these 170 ships loaded cargo in Lake Superior, and an additional 69 ships off-loaded cargo and continued operating on the Great Lakes. Again, a small number (13) of ships left the Great Lakes without loading cargo after their third port of call, and the remaining (56) ships continued to a fourth, or (rarely) fifth or greater, port of call. In each case, Lake Superior was the primary recipient of NOBOB ships that loaded cargo for their outbound voyage from their final port of call (Fig. 9.4).

Although some interannual variation was observed, general patterns emerged. First, between 68 and 82 percent of NOBOB vessels at their first port of call remained as NOBOB vessels at their second one (i.e., they dropped cargo and loaded ballast water at both ports; Fig. 9.4). This value dropped to between 26 and 75 percent at the third port visited. Most of the NOBOB vessels that discharged water at the second or third ports of call did so in Lake Superior. Lake Superior received more discharges of Great Lakes ballast water than all of the other lakes combined, and this pattern was consistent across years (Fig. 9.4). Thus, a disproportionate number of BOB and NOBOB vessels discharge ballast water into Lake Superior, even though Lakes Ontario and Erie are the initial ports of call of many NOBOB vessels.

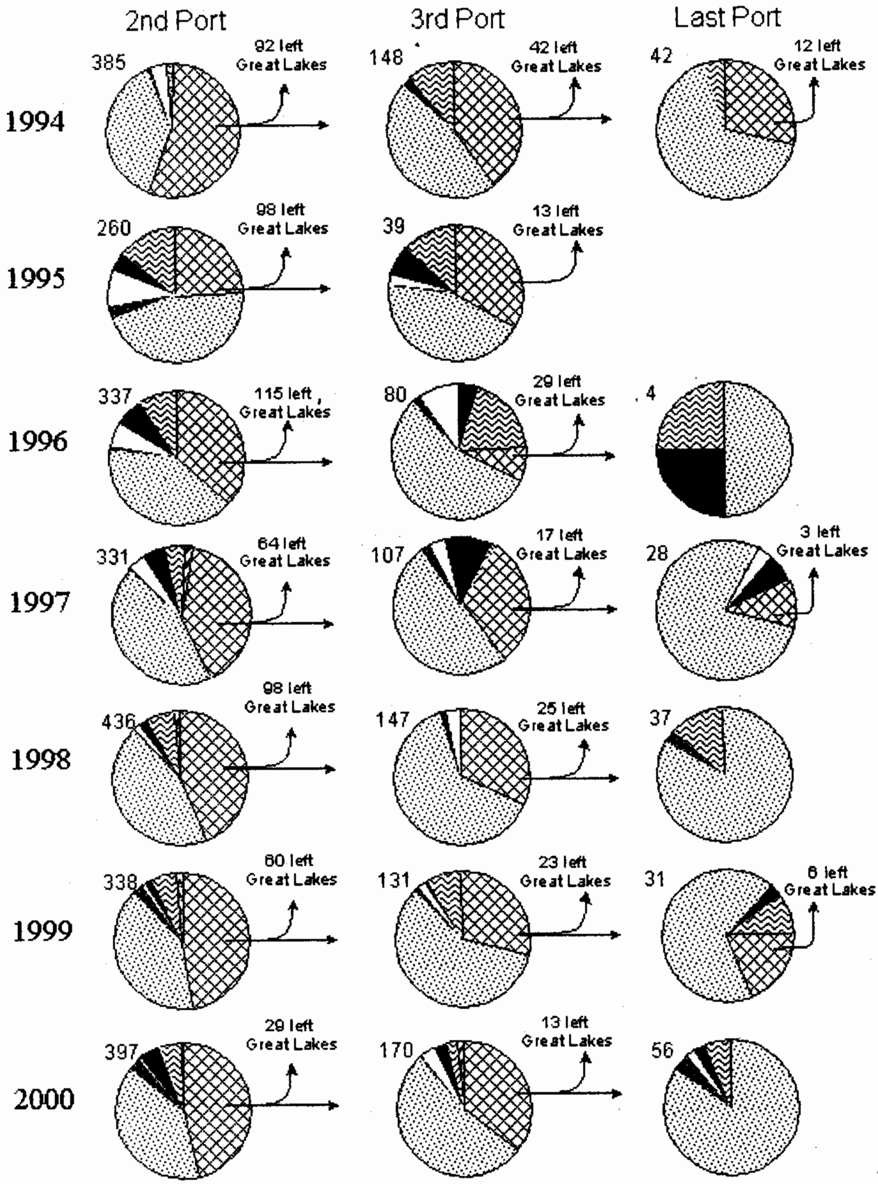

FIGURE 9.4. Spatial and temporal analysis of activity patterns of NOBOB ships entering the Great Lakes that (a) visited additional ports in the lakes before departure and (b) off-loaded cargo at their first port of call (see Table 9.2). All vessels are considered to have loaded ballast water during discharge of cargo in the first port of call. Each pie diagram illustrates the percentage of total ships (number above pie diagrams) that discharged additional cargo in that port of call (cross-hatched), or discharged Great Lakes ballast water in Lake Superior (stippled), Lake Michigan (dark stippled), Lake Huron (white), Lake Erie (black), Lake Ontario (wave), or at an unknown destination (diagonal). Many NOBOB ships left the Great Lakes for ports on the St. Lawrence River or other destinations without discharging Great Lakes ballast water into the Great Lakes; the number of these vessels is provided between pie diagrams. Activity of ships that discharged ballast at a fourth or later port is combined under "Last Port."

Propagule Pressure: The Null Hypothesis

In general, the propagule pressure model predicts that invasion success should be positively associated with the number and quality of inocula delivered to a recipient system. This propagule pressure model has been proposed as a possible explanation of NIS invasions in marine and other ecosystems (Carlton 1987, 1996, Carlton and Geller 1993, Ruiz et al. 1997, Kolar and Lodge 2001). Likewise, Ricciardi and MacIsaac (2000) reported that the pattern of NIS invasions of the Great Lakes by Ponto-Caspian species was consistent with the propagule pressure concept. So far, no effort has been made to quantify the relationship between NIS in the Great Lakes and propagule supply from donor regions. This analysis would require comprehensive information on the number of ships arriving to each of the lakes, the density and quality of organisms surviving transit in each of the ballast tanks, and the volume of ballast water discharged from each tank (see Carlton 1985). Ballast tanks in individual ships vary in location, size, accessibility, and biotic composition (Locke et al. 1991, 1993, Hamer et al. 2000, Bailey et al. 2003). Thus, comprehensive characterization of biological communities is a complex and difficult undertaking.

Ecologists have utilized both theoretical and empirical approaches to study determinants of invasion success, although most of these efforts have been directed at terrestrial ecosystems. For example, characteristics of the recipient community, notably its native biodiversity or natural or human-induced disturbance, are thought to affect invasion success (see Elton 2000). This area has received considerable examination in recent years (e.g., Levine and D'Antonio 1999, Lonsdale 1999, Shurin 2000, Levine 2000, Kolar and Lodge 2001). Availability of spatial or nutrient resources has also been related to invasion success (e.g., Burke and Grime 1996, Levine and D'Antonio 1999, Sher and Hyatt 1999, Stohlgren et al. 1999). In addition, invasion success may be influenced by biological characteristics and ecological interactions of potential colonists, including the number, size, and dispersing distance of individuals or resting stages from a population, or the order in which species invade communities (Drake 1993, Lodge 1993, Williamson 1996, Rejmánek 1996, Rejmánek and Richardson 1996, Grevstad 1999, Lonsdale 1999, Levine 2000, Shurin 2000, Kolar and Lodge 2002). It is likely that a combination of factors including an adequate and timely arrival of competent propagules, tolerance of physical and chemical conditions, and availability of spatial or nutrient resources are required for successful colonization by NIS.

We argue that the importance of propagule pressure is perhaps least understood, because of the difficulty inherent in quantifying the number of potential colonists involved in most natural invasions, as well as ethical and practical difficulties involved in experimentally manipulating NIS propagule pressure in most ecosystems (but see Grevstad 1999). Some propagule pressure models have been tested using inland lake systems. For example, Bossenbroek et al. (2001) developed mathematical models to predict invasions of zebra mussels (*Dreissena polymorpha*) based upon vector movement between invaded and noninvaded inland lakes, while Borbely (2001) did so for spiny water fleas (*Bythotrephes longimanus*) invading inland lakes in Ontario. These models have illustrated the importance of human vectors (trailered boats and contaminated fishing line, respectively) in the rapid dispersal of these Eurasian species in North America (e.g., see Johnson et al. 2001). Evidence has also accrued in terrestrial systems regarding the importance of propagule pressure. Lonsdale (1999), for example, reported that the number of nonindigenous plant species established in nature reserves was strongly related to the number of human visitors. It is important to note that transfer of propagules by vectors is but the first component of the invasion process, and that some ecosystems subjected to intense propagule pressure may, nevertheless, support few invaders if physical or chemical conditions are unfavorable (e.g., Chesapeake Bay; Smith et al. 1999). Nevertheless, the differential introduction of propagules is a key factor that must be accounted for in studies of invasion dynamics (Lonsdale 1999).

LAKE SUPERIOR: AN INVASION HAVEN?

Our study suggests that far more foreign BOB and NOBOB ships operating on the Great Lakes deballast in Lake Superior than on any of the other lakes. Although this lake has been the initial site of some NIS reports, most recently of ruffe (Pratt et al. 1992), the lower lakes dominate reports of initial NIS sightings (see Grigorovich et al. 2003a). Assuming that the frequency of vessel deballasting is a robust proxy of volume of ballast water discharged, more invasions of Lake Superior may have been expected. This discrepancy raises an interesting question: Is there something unique to Lake Superior that prevents establishment of NIS despite its relatively high inoculation rate, or have ecologists engaged in unintentionally biased reporting of NIS in the Great Lakes?

It is possible that Lake Superior is relatively inhospitable to NIS. Lake Superior is far less productive than the lower Great Lakes, and has a much greater ratio of limnetic to littoral habitat. Its thermal regime also exhibits much less seasonal variability than the lower lakes. Smith et al. (1999) reported that the upper Chesapeake Bay, despite receiving a large inocula of exotic species in ballast water, supports relatively few ballast-mediated NIS owing to adverse environmental conditions at the release sites. For Lake Superior, the relative lack of disturbance or invasions may also play a role. Disturbance of lower lakes or their watersheds, or presence of NIS that are "ecosystem engineers" (i.e., species that alter the physical/chemical properties of their environment) only in the lower lakes (e.g., zebra mussels), may have disproportionately facilitated invasions in these systems relative to Lake Superior (Simberloff and von Holle 1999, Ricciardi 2001).

Alternatively, Lake Superior may be more invaded than has been recognized, since many established NIS may remain undetected due to the large surface area of the lake and low sampling effort relative to the lower lakes. If this hypothesis is correct, intensive surveys should reveal heretofore unidentified NIS in the lake, particularly in regions where ballast water is discharged most commonly. A comprehensive survey of Lake Superior to test this hypothesis revealed a number of NIS range extensions from the lower Great Lakes, but no invaders new to the basin (Grigorovich et al. 2003b).

Although our intent was to provide a first approximation for ballast operations and associated propagule supply, it is likely that some of our assumptions, particularly those involving ballast water volume and content, are very coarse. For example, our assumption that vessels deballast only at the terminal port in the Great Lakes where they load cargo for the outbound journey may not be robust. BOB or NOBOB ships that discharge ballast en route to the terminal port could cause invasions in some of the lower lakes. Indeed, it has recently been reported that the sites of first discovery of NIS were concentrated around shallow, connecting channels in the Great Lakes, consistent with deballasting procedures that increase trim and improve maneuverability (Grigorovich et al. 2003a).

Mandatory ballast water exchange legislation covering the Great Lakes was implemented in 1993. This policy requires that all ships arriving from outside the EEZ (Exclusive Economic Zone) with freshwater exchange that water (or conduct an equally effective treatment) while on the open ocean in water not less than 2,000 meters deep and at least 320 kilometers from the nearest coastline (U.S. Coast Guard 1993). We assume that most freshwater organisms in the tanks would be purged, and the remaining ones killed when immersed in saline water. This procedure likely provides strong, but not absolute, protection of the Great Lakes from ballast-borne, freshwater invaders (Locke et al. 1993, MacIsaac et al. 2002). MacIsaac (1999) proposed that implementation of this policy should alter the pattern of invasions to the Great Lakes, with greater emphasis placed on invasions mediated by resting stages in ships' sediments, and less on ballast water itself. Resting stages are less likely to be purged with ballast water owing to their location in the bottom of the tanks, and less likely to be killed by saline ballast when the tanks are refilled. These resting stages could be expelled with ballast water in the Great Lakes, or later hatch when the tanks were filled with freshwater ballast. However, the relative importance of live organisms in ballast water, and of viable resting stages in ballast sediments, is only now being explored (Bailey et al. 2003). Even without considering resting stages in residual sediments, NOBOB vessels collectively appear to pose a greater risk of new invasions than BOB ships that comply with extant ballast water regulations (MacIsaac et al. 2002). Clearly, greater attention must be devoted to quantifying the volume and biological composition of ballast water delivered to each of the Great Lakes in order to provide a more rigorous test of the propagule pressure hypothesis.

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